Contrasting vegetation change (1974-2015) in hedgerows and forests in an intensively used agricultural landscape

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Running head: Opposite herbal changes in hedgerows and forests

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ABSTRACT

Questions: How did hedgerows and forests change in area between 1974 and 2015 and did hedgerows still show the same vegetation composition in 2015? To what degree did the vegetation change in hedgerows and how do these changes compare to changes in forests? What is the nature of the species that changed and, from these, can we make general inferences about possible drivers of change?

Location: The countryside in the municipality of Turnhout, province of Antwerp, northern Belgium.

Methods: Through a resurvey of 54 and 20 quasi-permanent plots in hedgerows and forests, respectively, we investigated shifts in the herb layer over the period 1974-2015. The plot-level mean Ellenberg Indicator Values (EIVs) were calculated and soil samples were taken in 2015. We compared diversity statistics and used GLMM to detect trends in species richness (SR) and EIVs. Via a NMDS-ordination based on the Sørensen dissimilarity, we compared shifts at the community level.

Results: Our study shows severe, however opposite changes in SR in forests and hedgerows. In forests, SR declined and a homogenization occurred. The shifts in EIVs indicate that forest vegetation evolved to more shade tolerant and nutrient demanding species, likely due to eutrophication combined with natural forest succession. In hedgerows, SR significantly increased. The species pool became more diverse and more heterogeneous. Changes in EIVs suggest a change towards more light demanding species, possibly caused by fragmentation of the network, and towards species indicative for nutrient rich habitats, benefiting from eutrophication.

Conclusions: In general, SR in hedgerows is higher than in forests in our studied region, being a suitable habitat for a wide range of plant species in the countryside.

However, the loss of almost 30% of the hedgerow habitat in 41 years, confronts us with the challenge of protecting the hedgerow remnants, in the interest of the agro-biodiversity.

KEYWORDS: Hedgerows; small forests; resurvey; temporal vegetation shift; historical plot data; species richness; Ellenberg indicator values; eutrophication; acidification; semi-permanent plots

NOMENCLATURE: Lambinon et al. (2015) for plants; Runhaar et al. (2004) for plant communities

ABBREVIATIONS:

- Al: aluminum
- Ca: calcium
- C: carbon
- EIVs: Ellenberg indicator values
- K: potassium
- Mg: magnesium
- N: nitrogen
- P: phosphorus
- SR: species richness

INTRODUCTION

Improving the integration of biodiversity conservation into key policies for agriculture and forestry is one of the six targets of the EU 2020 Biodiversity Strategy. These two sectors combined are involved in the management of 72% of the land in the EU, therefore playing a major role in the status of Europe's biodiversity (EC 2015). Semi-natural habitats in agricultural landscapes (e.g. grass strips, single trees,

63 hedgerows and forest patches) support the vast majority of the species diversity in
64 agro-ecosystems (Dover & Sparks 2000; Butet & Leroux 2001; Sullivan et al. 2012).
65 However, agricultural landscapes have drastically changed in many countries as farms
66 intensified their activities and became highly mechanized, at the expense of semi-
67 natural habitats (Baudry et al. 2000). When situated on the field borders, semi-natural
68 habitats may be removed to increase the field's cultivatable area or to allow for
69 merging adjacent fields into larger parcels. This trend has led to a decrease in the
70 diversity and abundance of fauna and flora in rural areas, sometimes even pushing
71 species towards local extinction (Suding et al. 2005; Jennings & Pocock 2009).

72 Among the semi-natural habitats in agricultural areas, hedgerows and small
73 forest patches provide relatively permanent habitats within a constantly disturbed
74 environment, acting as suitable habitats for many plant and animal species (Roy & de
75 Blois 2008; Decocq et al. 2016; Van Den Berge et al. 2018). They provide shelter,
76 breeding sites, habitats and food resources for a range of invertebrates (Burel 1989;
77 Duelli et al. 1990; Dover & Sparks 2000), birds (Dmowski & Koziakiewicz 1990;
78 Clergeau & Burel 1997; Hinsley & Bellamy 2000), small mammals (Tattersall et al.
79 2000; Butet & Leroux 2001; Gelling et al. 2007; Sullivan et al. 2012) and several
80 carnivore species (Šálek et al. 2009; Cervinka et al. 2013; Dondina et al. 2016). Here
81 we focus on the diversity and composition of the plant community, because of its
82 importance for the functioning of these ecosystems, including their relationship with
83 many trophic levels (Siemann et al. 1998; Steffan-Dewenter & Tscharntke 2001).

84 The largest contribution to plant diversity in both hedgerow (e.g. Deckers et al.
85 2004) and forest ecosystems (e.g. Gilliam 2007) originates from the herb layer.
86 Studies that aim at explaining what drives the spatial patterns of plant community
87 diversity and composition are widely available for forests (e.g. Brunet et al. 2000; Kolb

88 & Diekmann 2004; Houle 2007; Gazol & Ibáñez 2010) and hedgerows (e.g. Le Coeur
89 et al. 1997; de Blois et al. 2002; Deckers et al. 2004; Alignier & Baudry 2015; Van Den
90 Berge et al. 2018). However, for decision-making in management and conservation
91 strategies, we need to understand how these communities are changing over time as
92 well. The drivers of spatial patterns may be used to infer how environmental change
93 may cause the vegetation changes over time. Alternatively, resurveys of historical
94 vegetation records provide direct data on decadal changes in vegetation, although the
95 opportunities for such research are determined by the availability of high quality legacy
96 data. Such resurveys have been widely used to study forest understory vegetation
97 dynamics (e.g. Verheyen et al. 2017), but very few studies exist on temporal changes
98 in vegetation in hedgerows (but see Huwer & Wittig 2012; Staley et al. 2013; Litza &
99 Diekmann, 2017).

100 Syntheses across temperate forest vegetation resurvey studies have shown
101 that several global and local environmental changes have a strong impact on forest
102 plant diversity and composition. Changes include climate, altered forest management,
103 nitrogen deposition, and herbivore mammal abundances (Verheyen et al. 2012; De
104 Frenne et al. 2013; Bernhardt-Römermann et al. 2015; Perring et al. 2016). While it is
105 tempting to assume vegetation in hedgerows in the same regions of these studied
106 forests experiences similar changes, hedgerows actually form very distinct structures
107 and are managed differently. Because of their linear structure, they are far more
108 exposed to anthropogenic influences. Several studies (e.g. Schmucki et al. 2002;
109 Deckers et al. 2004) show that important drivers for hedgerow vegetation are the
110 adjacent land use and the agricultural practices in the neighboring fields; the use of
111 pesticides, the ploughing of the land and the harvest of the crops influence hedgerow
112 vegetation in a chemical or physical way. This clearly illustrates the potential value of

113 simultaneously focusing on temporal vegetation change in both hedgerows and forests
114 in the same study area.

115 Here we present the results of a vegetation resurvey study (1974 – 2015) in
116 hedgerow and forest plots in an intensively used agricultural landscape in northern
117 Belgium. The countryside in this region has a high degree of urbanization and
118 agriculture has further intensified and increased in area between the surveys. We
119 determined the shifts in plant community diversity and composition over the past four
120 decades, including only understory plant species in our analysis, as woody species
121 are often more driven by management choices than by natural processes (French &
122 Cummins 2001). With these data we will answer the following research questions:

123 (1) How did the hedgerow and forest habitats change in area between 1974 and
124 2015 and did hedgerows still show the same vegetation structure like 41 years
125 ago?
126 (2) To what degree did the understory vegetation change over a period of 41 years
127 in the hedgerows and how do these changes compare to changes in forest
128 patches in the same region?
129 (3) What is the nature of the species that changed the most and, from these, can
130 we make some general inferences about the possible drivers of change?

METHODS

Study area and study systems

The municipality of Turnhout (province of Antwerp, northern Belgium, Figure 1) has a total area of 56 km², 16.42% of which are forests and 55.86% are agricultural landscapes (based on the CORINE methodology, European Environment Agency 2013). Altitude varies between 18 and 35 m above sea level (Van der Veken et al. 2004). The climate is temperate with a total annual rainfall of 755 mm and an average temperature of 10.1 °C. The region is dominated by Aeolian sandy soils, deposited during the last glacial period.

About three quarters (76%) of the studied hedgerows in the countryside (*anno* 2015) are elevated (woody vegetation on artificial ground, so called 'wooded banks') and the remainder are at the same height as the surrounding land; however, all will be referred to as 'hedgerows'. The average width is 3.1 ± 1.7 m and the average length is 183.1 ± 135.4 m. *Quercus robur, Frangula alnus, Quercus rubra* and *Betula pendula* are the most frequent species in the tree and shrub layer (present in 94.4; 31.5; 24.9 and 24.9% of the hedgerow plots, respectively). The studied forest patches have an average area of 1.94 ± 1.51 ha; most common species in the tree layer are *Quercus robur* (in 55.5% of the plots) and *Betula pendula* (40.0%). *Sorbus aucuparia* (60.0%) and *Frangula alnus* (50.0%) are the most frequent species in the shrub layer.

Vegetation (re)sampling

During the summer of 1974 (July and August), a phytosociological vegetation study was carried out in Turnhout (Vanderschaeve 1975). The vegetation was recorded in a total of 81 plots in hedgerows and 26 plots in forests. Selection of hedgerows was done using this criterion: they showed a well-developed herb, shrub and tree layer to avoid already degraded hedgerows. The forest patches, on the other

156 hand, were randomly selected in the landscape. A representative part of the vegetation
157 was recorded via plots varying between 25 - 150 m² and 60 – 150 m² for hedgerows
158 and forests, respectively. The plot size was assigned to every single hedgerow and
159 forest according to several a priori chosen sample sizes. Sizes were defined during an
160 exploratory study (before the actual study took place) based on the "minimal area
161 principle": The minimal area of a community is the smallest area on which the
162 community can develop its characteristic composition and structure (Cain & Oliveira-
163 Castro 1959). Plots were chosen at a position in the middle of the hedgerow length
164 and randomly in the forest patch. All species in the herb (< 0.5 m tall), shrub (< *ca.* 3
165 m tall) and tree layer were identified and their percentage cover was estimated as a
166 measure of their abundance (Barkman scale; Barkman et al. 1964). All plots were
167 indicated on a topographical map and can be considered quasi-permanent (Kapfer et
168 al. 2017).

169 During the summer of 2015 (July and August), the plots were revisited. We used
170 the topographic map from the original study (scale 1/25000, marked with hand drawn
171 plots) in combination with current aerial pictures with the digitized plots obtained via
172 QGIS (QGIS Development Team 2016. Software version Desktop 2.18.18, QGIS
173 Geographic Information System. Open Source Geospatial Foundation Project). In this
174 way, we were able to relocate the sampled plots in a very accurate way.

175 In the field, each hedgerow was classified based on the general degradation
176 status along its complete length (Appendix S1): 'intact' (hedgerow with well-developed
177 herb, shrub and tree layer), 'degraded' (hedgerow with depleted or missing tree layer
178 or shrub layer, mostly due to cutting) and 'lost' (hedgerow cleared). Also some
179 additional attributes were recorded: whether or not the hedgerow was a wooded bank,
180 presence of a ditch, and adjacent land use (arable land, forest, brushwood, grassland,

paved road, dirt road, garden, build-up area). We resurveyed 54 vegetation plots (3260 m^2 in total) in the degraded and intact hedgerows analogous to the 1974 recordings (27 plots had disappeared). Likewise, 20 plots (1985 m^2 in total) in the forests were resurveyed (three plots had disappeared and three plots were no longer accessible). Some of the hedgerows became more narrow (*n = 9*) or wider (*n = 6*) and in both cases we respected the original plot size by adjusting the length of the plot. In the few occasions (*n = 5*) that the original plot was no longer located within the hedgerow (hedgerow was shortened) we relocated it within the remnants, in the middle of the current length. Indeed, even though the exact location of the original sampling plot is not precise, still accurate vegetation changes can be determined (Kopecký & Macek 2015). We estimated the abundance of all species in the herb, shrub and tree layer in percentage classes (Hennekens 2009). Since the original survey used the Barkman abundance scale, data were converted into percentage classes *sensu* Hennekens (2009) (Appendix S2).

Environmental variables

Because in the original study no soil samples were taken, we used Ellenberg indicator values (EIVs) to explore how environmental conditions have changed between the old and recent vegetation records. For each plot, we calculated unweighted mean EIVs for productivity (N), soil reaction (R), soil moisture (F) and light availability (L). We decided to use unweighted values to account for a possible consistent difference in abundance estimates between observers. Ellenberg values are known to be good proxies for these environmental conditions (Diekmann 2003).

Besides, we collected soil samples in a subset of the plots in both ecosystems during the summer of 2016 to allow for a better interpretation of patterns in EIVs in terms of the measured soil chemistry. A fraction of 40% of the plots was selected along

a gradient in mean Ellenberg R-values (weighted sample: hedgerows: *n = 21*, forests: *n = 9*). In each plot, we collected a mixed soil sample consisting of eight subsamples. All subsamples were taken with a gouge auger in the 0-10 cm mineral topsoil layer after removing the organic litter layer. Sample positions within the plot were randomly chosen over the entire plot area, but at least 1 m distance from trunks and edges to avoid edge and 'trunk' effects. In the laboratory, oven-dried (40 °C for a period of 48 hours) and sieved soil was mixed in water in a 1/5 ratio, shaken for five minutes and left to stand for two hours. The pH-H_2O-value was measured using a pH meter with Ross Sure-Flow combined electrode (Orion, USA). The carbon (C) and nitrogen (N) concentrations were determined with a vario MACRO cube (Elementar, Germany). The phosphorus (P) and base cation concentrations (potassium (K), calcium (Ca), magnesium (Mg), and aluminum (Al)) were measured after an ammonium lactate-EDTA extraction.

Data analysis

Structural changes

Surface loss of forests and hedgerows over the 41-year period was calculated via QGIS. The association of the hedgerow status (lost, degraded, intact) with the features adjacent land use (converted to dummy variables), the presence of a ditch and whether or not the hedgerow was elevated was tested via a Chi^2-test.

Vegetation changes and ecological characteristics of species

We looked into the ecology of the species by allocating every species to a particular species group *sensu* Runhaar et al. (2004) (pioneer species, grassland species, tall herb species and forest species) and looked up their EIVs *sensu* Ellenberg et al. (2001). For each species group, we counted the number of species (species richness = 'SR') and the mean abundance of these species in each plot. The plot-level mean EIVs were also calculated.

To illustrate the conservation status of the species in our inventories, we allocated a threat status to every species according to the red list for Belgium (Van Landuyt et al. 2006). Furthermore, we classified species according to their observed change in frequency over time: species that had disappeared by 2015 ('lost species'), species that appeared since 1974 ('new species'), and species that are common in both inventories. Among these common species, we classified 'losers' and 'winners' (present in 10% less and 10% more plots compared to 1974, respectively).

For both forest and hedgerow plots, we considered the size of the total species pool in each period (γ diversity), rarefied to the number of plots in 2015 (Chao et al. 2014). So, by interpolation, the expected γ diversity could be correctly compared between the years (Colwell et al. 2004). Absolute numbers of species (in total and per species group) of the species pools in the two periods were compared via a Chi^2-test.

Local plot-level taxonomic diversity (i.e. α diversity) was estimated as a diversity of order zero (species richness; ^0D) and order one (exponential of Shannon; ^1D), the latter to take into account SR and abundance of each species within the plot. By taking the exponential of the Shannon index, the index is converted into an effective number of species, in this way two plots with equal diversity also acquire the same value. This facilitates the interpretation of the results (Jost 2006). Compositional differences between plots were assessed with pairwise dissimilarity metrics (β diversity). A Sørensen dissimilarity (β_{Sor}) was used to quantify overall compositional differences and was further partitioned into its turnover (β_{Sim}) and nestedness (β_{Nes}) components to discriminate between species replacements across plots and richness differences leading to nestedness patterns across plots, respectively (Baselga 2010). The significance in differences for these diversity statistics between the two years was tested with a paired Wilcoxon signed-rank test (i.e. nonparametric test, when the data

were not normally distributed) or paired t-test (i.e. parametric test, when the data were normally distributed).

We used Generalized Linear Mixed-Effects Models (GLMMs) via the glmer function in the 'lme4' package (Bates et al. 2015) with Poisson distribution to detect significant trends in all these response variables (overall SR, SR of the four species groups, EIVs) over the two periods and between the two ecosystems (hedgerow and forest). Plot size was initially included in the models to check its influence on the response variables, but due to its small effect, we decided to leave it out in the final analyses. Plot identity was used as a random effect to account for the paired nature of the design (the same plot was recorded in two time points). To be able to plot the significance of the differences over time between the response variables within one ecosystem (i.e. forest or hedgerow), we used a paired t-test, as we could not use p-values from the models because of significant *year x ecosystem* interactions.

In order to compare the vegetation shifts at the community level, we performed a Non-metric multidimensional scaling ordination (NMDS) via the metaMDS function in the R package 'vegan' (Oksanen et al. 2015) with three a priori chosen dimensions for the hedgerows (stress was too high with two), two a priori chosen dimensions for the forests, and maximum 50 iterations. Our ordination was based on the Sørensen dissimilarity matrix of the full vegetation data sets (sets of 1974 containing only the plots that could be revisited). Significance of the effect of time on composition was tested with a permutational multivariate analysis of variance (PERMANOVA) on the same dissimilarity matrix (2000 permutations). An analysis of the multivariate dispersion (betadisper function in the vegan package) was performed to examine whether the multivariate spread was the same for the two periods or differed significantly. Correlations between the mean EIVs of the vegetation in the hedgerow

and forest plots and the two axes of the NMDS-analysis was assessed with the envfit function (also from the vegan package) and visualised by plotting the vectors onto the NMDS plots.

For the hedgerow plots, the influence of its status (intact vs degraded) on the average SR in the herb layer and on the species group-specific diversity, as well as on the average EIVs was tested with a t-test (when normally distributed) or Wilcoxon Signed-rank test (nonparametric statistics).

Soil characteristics

The significance in differences for all measured soil characteristics between the two ecosystems was tested via a Wilcoxon signed-rank test, as these variables were not normally distributed. Spearman rank correlations were performed between the soil characteristics and mean EIVs of the plots for forests and hedgerows (only for the year 2015).

All statistical tests were performed at the 5% level of significance, in R 3.2.3 (R Foundation for Statistical Computing, Vienna, AT).

297 **RESULTS**

298 **Structural changes**

299 The total surface of the studied forests decreased by *ca* 6.9%, from 45.88 ha in
300 1974 to 42.71 ha in 2015. For the studied hedgerows, we found that the total length
301 decreased by *ca.* 28.2%, from 20.93 km in 1974 to 15.02 km in 2015. Only 64.5% of
302 the remaining network length was coded as 'intact' (9.69 km) and the remainder was
303 'degraded' (Figure 1). Hedgerows without a ditch were more likely to become lost ($p <$
304 *0.05*). Of the remaining hedgerows, the wooded banks were more likely to remain
305 intact ($p < 0.001$). The status of the hedgerow (intact, degraded, lost) was not related
306 to the current adjacent land use.

307 **Vegetation changes in the hedgerow and forest plots**

308 For hedgerows, the rarefied γ diversity significantly increased from 1974 to
309 2015 ($p < 0.001$, Table 1). There were 53 species common to both surveys, among
310 which nine winners and eight losers. 26 species were lost between the two surveys,
311 and 67 species were new. In 1974, the species pool consisted for 93.6% of common
312 species that are currently not threatened and 6.4% declining species: *Calluna vulgaris,*
313 *Erica tetralix*, *Potentilla erecta, Salix repens, Solidago virgaurea* and *Melampyrum*
314 *pratense*. In 2015, percentages in hedgerows shifted even more towards not
315 threatened species (96.7% of the pool) and less declining species (2.5%: *P. erecta,*
316 *C. vulgaris* and *M. pratense*) and one threatened species (*Juncus tenageia*). New
317 species were mainly native except for *Conyza canadensis*, *Galinsoga quadriradiata*
318 and *Impatiens parviflora* and scored generally high in EIVs (e.g. *Eupatorium*
319 *cannabinum, Cirsium vulgare and Lamium album* with L-value = 7, 8, 7; N-value = 8,
320 8, 9, respectively).

At the plot level, the mean α diversity ^0D and ^1D significantly increased in hedgerows (Table 1). In terms of compositional variation, the mean Sørensen dissimilarity ($\beta_{Sør}$) increased slightly between 1974 and 2015, though the individual turnover (β_{Sim}) and nestedness (β_{Nes}) components showed no significant change (Table 1).

In the intact hedgerows, the overall plot-level diversity (^0D and ^1D) and the species group-specific diversity (forest species; grassland species; tall herbs and pioneer species) were not significantly higher compared to the degraded hedgerows (*all comparisons* $p > 0.05$). Diversity in both the intact and degraded hedgerows was significantly higher in 2015 compared to 1974 (both overall species richness and species group-specific diversity, *all comparisons* $p < 0.001$). Mean EIVs in intact and degraded hedgerows did not differ significantly nor changed in a different way over time (*all comparisons* $p < 0.001$).

In forests, the γ diversity decreased, however, not significantly ($p > 0.05$, Table 1). There were 15 species common to both surveys (nine among which were losers), 33 lost species and 9 new species. 91.7% of the species in forests in 1974 were not threatened and 8.3% were declining (*C. vulgaris* and *E. tetralix*). In 2015, only common species occurred in the forests. New species were native except for *I. parviflora* and scored generally low in L-values and high in N-values (e.g. *Geum urbanum* and *Ribes rubrum*). At the plot level, the mean α diversity ^0D and ^1D decreased in forests. Also both $\beta_{Sør}$ and β_{Sim} decreased significantly (Table 1).

The shift in EIVs at the community level is visualized in the NMDS analysis (*Stress = 0.20*): hedgerow surveys from 1974 and 2015 are clearly distinct on the first two axes (*PERMANOVA Pseudo-F = 9.8, p < 0.001*, Figure 2) and on the first *vs.* the

345 third axis (Appendix S3). The variance between the two years was almost the same
346 (*ANOVA, $p > 0.05$*). Correlations between the vectors of the EIVs and the (co)ordinates
347 of site projections onto the first two axes are all significant (*$p < 0.001$*). The first axis is
348 strongly positively correlated with the N- and R-values (*$\rho = 0.96$* and *$\rho = 0.82$*,
349 respectively), to a lesser extent to the F value and negatively correlated with the L-
350 value (*$\rho = 0.55$* and *$\rho = -0.50$*, respectively). The second axis is stronlgy positively
351 correlated with the L-value (*$\rho = 0.82$*); and to a lesser extent to the F-, R- and N-values
352 (*$\rho = 0.77$, $\rho = 0.56$, $\rho = 0.26$, respectively*). Also forest surveys from 1974 and 2015
353 were easily distinguished from each other in the NMDS-ordination (*Stress = 0.16,*
354 *Pseudo-F = 6.0, $p < 0.001$*). However, variation between the two years was not the
355 same (*ANOVA, $p < 0.05$*), possibly explaining a part of the difference between the two
356 years.Correlations between the vectors of the EIVs and the two axes were all
357 significant (*$p < 0.001$*), except for the F-value (*$p > 0.05$*). The first axis is strongly
358 positively correlated with the F-, R and N-values (*$\rho = 0.99$, $\rho = 0.96$ and $\rho = 0.93$,*
359 *respectively*). The second axis is strongly positively correlated to the L-value (*$\rho = 0.99$,*
360 Figure 2).

361 **Ecological characteristics of the species**

362 In the species pool of hedgerow plots, representation of forest and pioneer
363 species significantly increased (*$p < 0.05$*); grassland species and tall herbs decreased.
364 In the species pool found in the forests plots in 2015, pioneer species did not occur
365 anymore and distribution had shifted towards more forest species and tall herbs and
366 significantly less grassland species (*$p < 0.05$*).

367 At the plot level, the mean number of forest species, grassland species, tall
368 herbs and pioneer species consistently increased in the hedgerow plots and
369 decreased in forest plots (Figure 3). Temporal patterns in the number of the species

groups were different between hedgerows and forests (*year x ecosystem interaction* $p < 0.01$). In both periods, hedgerow plots contained significantly more grassland species and tall herbs compared to forest plots and comparable amounts of forest species and pioneer species (Figure 3). Results for mean abundances of each species group were qualitatively similar, except for forest species and tall herbs in forests, which increased their abundance whereas their richness decreased (Appendix S4).

The mean EIVs changed consistently over time in hedgerow and forest plots: N-, R- and F-values increased whereas L-values decreased, although none of the shifts were significant (Figure 4). N-values and R-values were strongly correlated across plots in both ecosystems (*forests:* $\rho = 0.76$, $p < 0.05$; *hedgerows:* $\rho = 0.71$, $p < 0.001$).

Soil characteristics in hedgerows and forests differed significantly (Appendix S5). Soil pH was significantly higher in hedgerow plots compared to forest plots (4.7 ± 0.6 *vs.* 4.1 ± 0.3, respectively). In hedgerows, pH-values in almost all plots (76%) ranked above 4.2 and thus above the Al buffer range (Ulrich 1983). In forests, 78% of the plots showed pH-values below 4.2 units. In addition, ammonium lactate-P and base cation concentrations (K, Ca, and Mg) were significantly higher in hedgerow plots compared to forest plots. Only C, N and Al concentrations did not differ significantly across plots in both ecosystems (Appendix S5). Furthermore, N-values in both forest and hedgerow plots were positively correlated with the concentration of P in the soil (Appendix S5). In forest plots, R-values were also positively correlated with P concentrations and mean N-values were positively correlated with the concentration of K in the soil (Appendix S5). Mean R-values in hedgerow plots were negatively correlated with the concentration of Al. None of the EIVs were correlated with soil pH nor N, C, and Mg concentrations.

DISCUSSION

All over Europe, fragmentation of semi-natural habitats has continued to increase during the last 20 years (EEA 2011). Habitat patches are broken apart, reduced in size and become increasingly isolated. Consequently, the remaining ecological network provides less and less connectivity, negatively affecting ecological communities (EEA 2011). Also in our studied landscape, forest area has been lost and one third of the hedgerows was completely destructed over 41 years. However, in the remaining plots, (still) many plant species were found; hedgerow plots in particular hosted surprisingly many species (120 different species in total). In both ecosystems there were losses over the last four decades; the more threatened and rare species declined at the expense of generalists. Generally speaking, plant species richness in forests decreased clearly, whereas hedgerows strongly increased in plant diversity.

Hedgerows *vs.* forest patches in the agricultural landscape

Comparing both habitat types, we found clearly higher diversity in plants in hedgerows compared with forests. The species pool in hedgerows was much larger and the distribution among species groups more balanced. Even though the sampled area in hedgerows and forests was not the same (bigger sampled area in hedgerows) so the comparison is not completely fair, it is clear that hedgerows offer suitable habitats to more different plant species than do forests in our studied region. Hedgerows are typical edge habitats. They are structurally more heterogeneous then core habitats, including shaded parts as well as forest edge conditions. There is also variation in exposure to solar radiation and wind, creating even more niches (Critchley et al. 2013; French and Cummins 2001). In addition, hedgerow soils seem to have more suitable soil properties for plant growth compared to forest soils in our studied region, as we found higher pH and higher availability of P and basic cations. The soil

420 characteristics in our studied forests demand a more customized life strategy of the
421 vegetation resulting in a smaller species pool.

422 **Biodiversity decrease in forests**

423 The plant biodiversity in the forest fragments in this agricultural landscape
424 decreased over the past four decades, in terms of local diversity within forests as well
425 as compositional variation between forests. Similar patterns have been shown in
426 several other forest resurvey studies (e.g. Keith et al. 2009, but not in others e.g.
427 Verheyen et al. 2012). In our study, forest communities clearly shifted towards more
428 shade tolerant species (lower L-value), at the expense of the more light demanding
429 grassland species and pioneers – the latter totally gone in 2015. This indicates that
430 forest succession might be ongoing. Most of the forests in the Campine region were
431 planted during the 19th or 20th century, when afforestation of former heathland took
432 place (Kint et al. 2010). Young forests growing older entails the establishment of more
433 shading trees and shrubs, being a possible driver of plant biodiversity loss, as only
434 well-adapted species can survive beneath a densely closed forest cover (Baeten et al.
435 2009).

436 In addition, the subtle community shift towards more nutrient demanding
437 species (higher N-value), indirectly indicates an increase in the availability of nutrients.
438 Natural forest succession might also be a possible explanation here, as in general,
439 this leads to eutrophication of the soil via the building up of organic matter (Hédl et al.
440 2010). The correlation of the N-values of the vegetation with the amount of P and K in
441 the soil – these two elements being main elements of fertilizers – also indicates
442 eutrophication is ongoing. Fertilization of adjacent fields, combined with atmospheric
443 deposition of reactive nitrogen from agriculture, traffic and industry (Bobbink et al.
444 2010) is probably contributing to the eutrophication of the forests. Although

atmospheric deposition has declined in recent decades, the long-term accumulation has caused nitrogen-saturated ecosystems (De Schrijver et al. 2007). This eutrophication is mirrored as a decline in forest vegetation richness, at the expense of more specialized forest species, such as *Teucrium scorodonia* and *Vaccinium myrtillus*.

Deposition of atmospheric nitrogen and other acidifying pollutants, can also lead to forest soil acidification (Heisner et al. 2003; Van Calster et al. 2007; Baeten et al. 2009). Indeed, acidification is a widespread pattern in agro-ecosystems, mainly caused by the input of organic fertilizers that contain ammonium, which is oxidized to nitrate by which protons are released (Barak et al. 1997). Surprisingly, we found higher R-values for the forest community in 2015, whereas an acidification signal would be indicated by a decrease in R. However, there is no evidence for an ongoing deacidification nor acidification, as mean R-values were actually not correlated to the measured pH-values. R-values were, just like N-values, correlated with the amount of P in the soil, and both R- and N-values showed positive covariation. Such correlations between indicator values can create problems in the interpretation of ecological resurvey studies (Diekmann 2003; Naaf and Kolk 2015; Litza and Diekmann 2017). The pH-values in our resurvey were all situated in the Al buffer range (buffering stage "Al hydroxides": pH 4.2-2.8), which is characterized by a high bioavailability of Al (Ulrich 1983; Appendix S5). Inhibition of root growth and function is the primary effect of Al on plants. Owing to Al inhibition of primary and lateral root growth, the growth of root systems is strongly reduced, negatively affecting the survival chances of a species (Lukac & Godbold 2011). Even though we cannot compare pH-values over time, it is plausible that Al toxicity might have become a factor decreasing species diversity in the forests.

Biodiversity increase in hedgerows

Hedgerows became more diverse (both in overall plant diversity and in diversity of the forest species, grassland species, tall herbs and pioneers) and taxonomically more heterogeneous over time. This is quite a different result compared to the findings of previous hedgerow resurvey studies, which have consistently reported a decline in overall diversity (Huwer and Wittig 2012; Staley et al. 2013; Litza and Diekmann 2017) and most also reported an increasing homogenization of the vegetation (e.g. Staley et al. 2013). However, in our study, a transition phase might be ongoing where original vegetation is still present and newly established vegetation increases the number of species, but reorganization may follow.

Fragmentation might be one of the underlying factors in our study of maintaining and increasing beta diversity. Due to fragmentation, the edge-to-core ratio of the hedgerows increases even more – being already quite high, as they are typical edge habitats – when they are shortened or when gaps appear. Edge habitat is influenced more profoundly by the surroundings, supporting the establishment of disturbed vegetation such as pioneers (Runhaar et al. 2004). This might also explain the shift in the species pool towards a composition of more light demanding species (higher L-value).

Over time, also more species indicative for nutrient rich soils found their way to the hedgerow habitats, resulting in higher diversity. Again, eutrophication seems to be the logical explanation for this shift (cf. also the findings of Staley et al. 2013; Litza and Diekmann 2017). Hedgerows – especially those located in agricultural fields – are exposed to high inputs of fertilizers. Moreover, crop plants in bordering agricultural fields tend to grow less strong because the shading of the hedgerow, using less of the applied fertilizers, possibly causing accumulation of fertilizers in the soil over time

(Mette 1994). Additionally, just like forests, hedgerows are exposed to atmospheric depositions causing further eutrophication and acidification of the ecosystem. The edge character of the hedgerows causes locally an increased wind turbulence, which allows an even higher nitrogen deposition and deposition of other acidifying pollutants compared to the deposition inside forest patches. The observed shift of hedgerow vegetation towards species with higher R-values would indicate a deacidification is ongoing, even though they were not correlated to the measured soil pH. Also Litza and Diekmann (2017) stated that in their studied hedgerows, the increasing nutrient availability (reflected in increasing mean N) overruled the responses of species to pH, as they found proof that soil pH decreased over 50 years while the mean R-values increased. The pH-values in our resurvey were almost all above the Al buffer range. However, the proportion of acid-tolerant species was strongly determined by Al concentrations in the soil (strong negative correlation between R-value of the vegetation and Al concentration in the soil). If soil acidification continues, Al-toxicity might become a problem for plant species diversity in the hedgerows.

In our studied hedgerows, a shift of typical vegetation well suited within the syntaxa one had in mind for the original thesis, to a kind of frame communities with the presence of non-typical species (e.g. more grassland species and pioneers), may have occurred. This shift may have resulted in a biodiversity increase for now. However, challenges such as climate change, further fragmentation and immigration of new plant species can enhance reorganization and dominance of single species in the future (Smith et al. 2009). Follow-up research remains needed to study the temporal vegetation changes in hedgerows and forests in intensively used agricultural lands.

CONCLUSION

In a period of four decades, major changes in both the structure and species composition of our semi-natural habitats in the countryside occurred. Over time, several threatened species were lost in both ecosystems, as eutrophication may have led to a shift towards more competitive species typical for nutrient rich habitats. Additionally, forest succession led to a strong light-determined diversity decline, whereas hedgerows hosted significantly more species in 2015. These different temporal vegetation shifts demonstrate the importance of considering diversity patterns in more than one ecosystem at once at a landscape scale, to get a broader idea about vegetation changes at this scale.

Irrespective of the fact that species richness in hedgerow networks is not declining and the existing species pool is relatively species rich, it is striking that in a period of 41 years, almost one third of the studied length of the network was cleared. In 100 years from now, hedgerows may be gone if this 'business as usual' continues (i.e. when considering a constant loss of 150 m/year). Even though it is more likely that only a specific proportion and not all of the hedgerows will be lost in our studied agro-ecosystem, it is clear that we are losing significant amounts of hedgerows. They are clearly suitable habitats to many different plant species, hosting a bigger variety of functional plant species groups and more threatened species than forests in our studied region. Proportionally much more hedgerow habitat than forest habitat disappeared during our studied period. The extent to which we will do efforts to ensure conservation of these hedgerows, will definitely determine the future biological content of the landscape.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1. Intact, degraded and lost hedgerows.

Appendix S2. Abundance scale *sensu* Barkman and *sensu* Hennekens.

Appendix S3. NMDS-ordination diagrams of hedgerow plots (Axis 1 *vs* Axis 3; Axis 2 *vs* Axis 3).

Appendix S4. Shift in abundance of considered species groups.

Appendix S5. Results of soil analyses (2015).

TABLES AND FIGURES

Figure 1

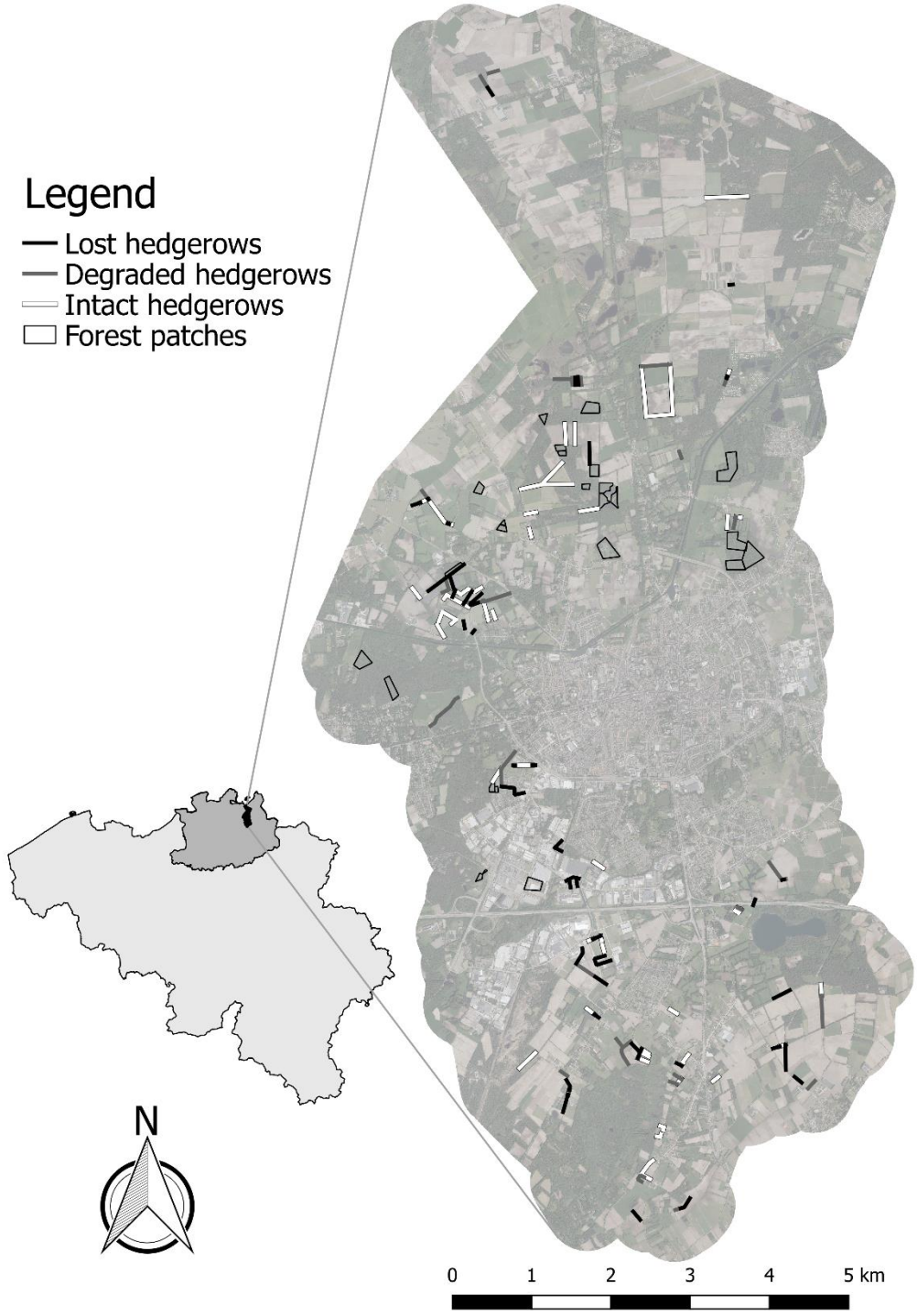

Figure 1. Study area. Map showing the location of the study area in the province of Antwerp in the north of Belgium. The municipality of Turnhout is presented in detail with indication of studied hedgerows and forests. Source aerial picture: Geopunt Vlaanderen.

Figure 2

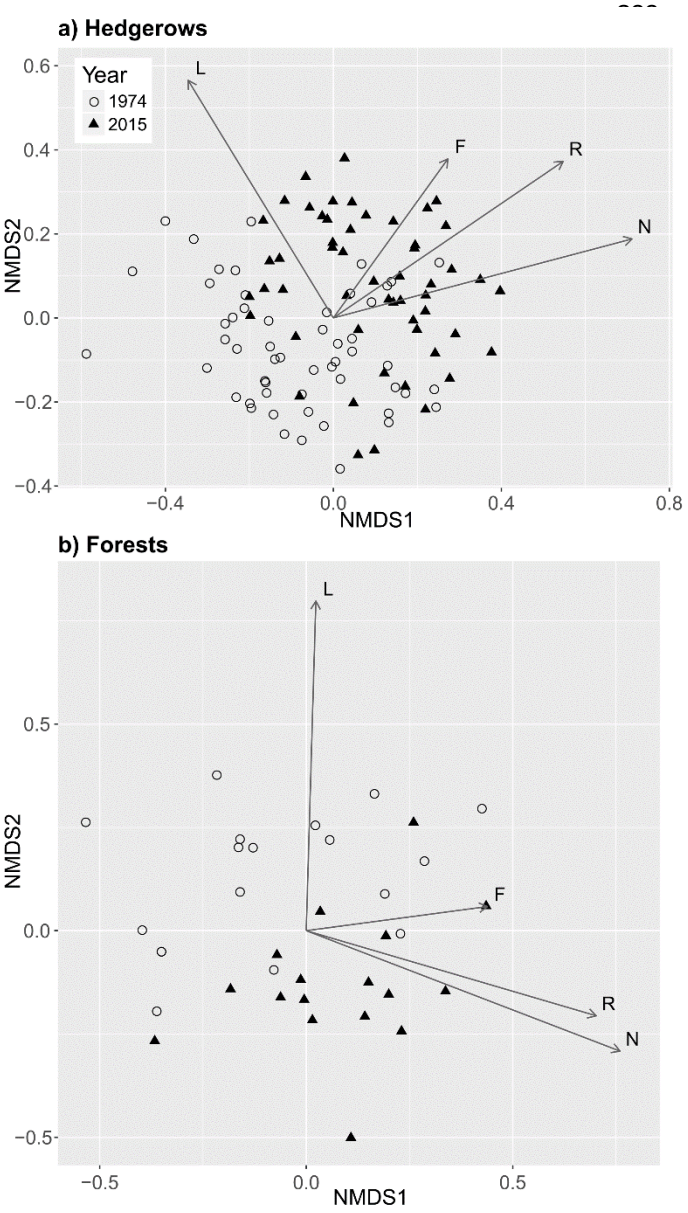

Figure 2. NMDS analysis showing temporal vegetation shift. NMDS-ordination diagrams (ordination based on Sørensen dissimilarity) for hedgerow plots (a) and forest plots (b) are shown. The diagrams include the original plots (*n = 54* for hedgerows and *n = 20* for forests) and the resurveyed plots (*n = 54* for hedgerows and *n = 20* for forests). The vectors generated via the 'envfit' analysis (function in the R package vegan) indicate the correlation of the axes with the Ellenberg indicator values.

Figure 3

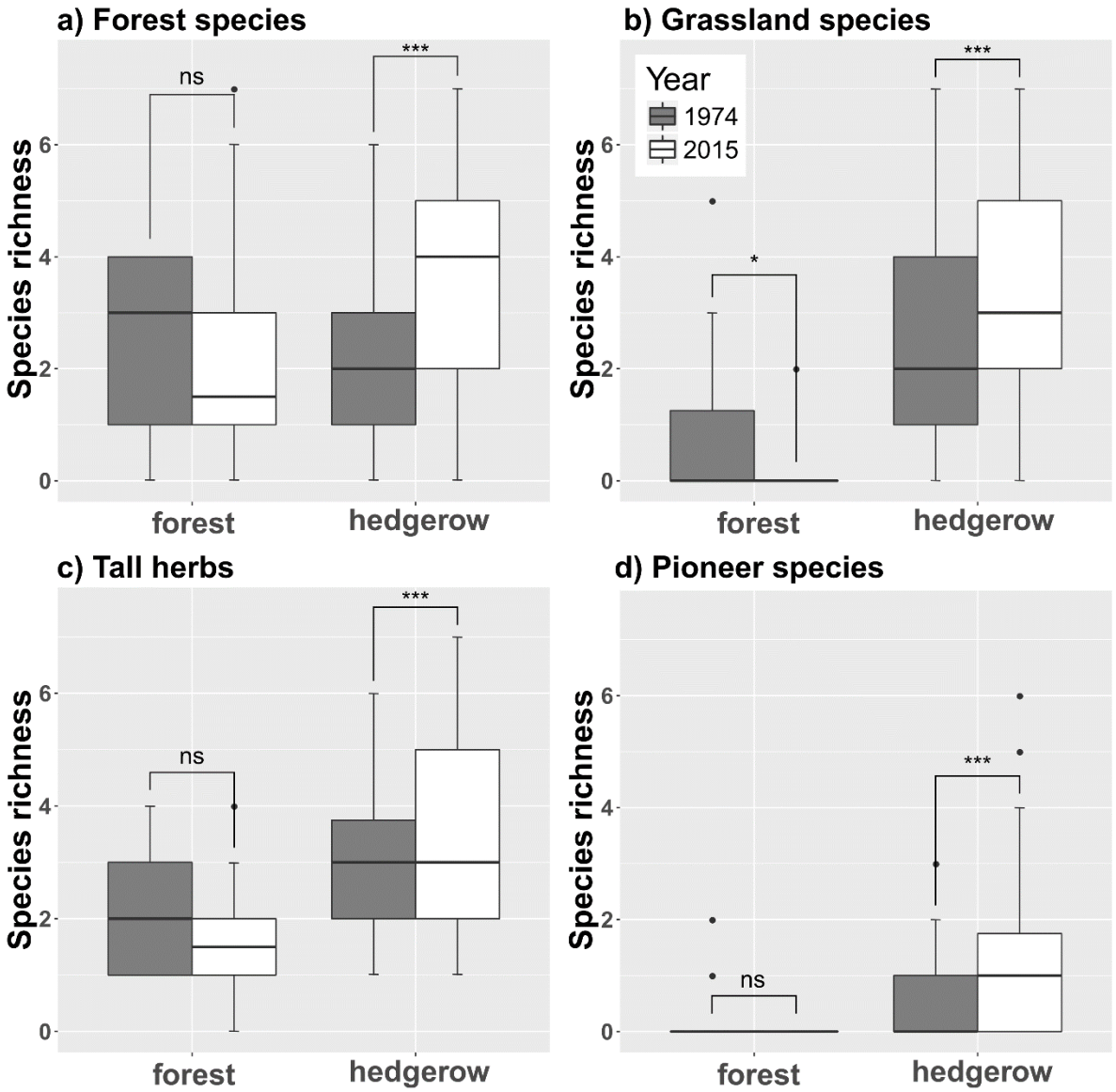

Figure 3. Temporal vegetation change. Changes in mean species richness in hedgerows and forests between 1974 and 2015 for forest species (a), grassland species (b), tall herbs (c) and pioneer species (d) (*sensu* Runhaar et al. 2004). The boxes indicate the 25% and 75% quartile, with a median line and 2 whiskers showing the 10% and 90% quantiles. Significant differences in species richness as derived from paired t-tests are indicated with asterisks (*p-value levels ns: not significant; ***: p ≤ 0.001*).

Figure 4

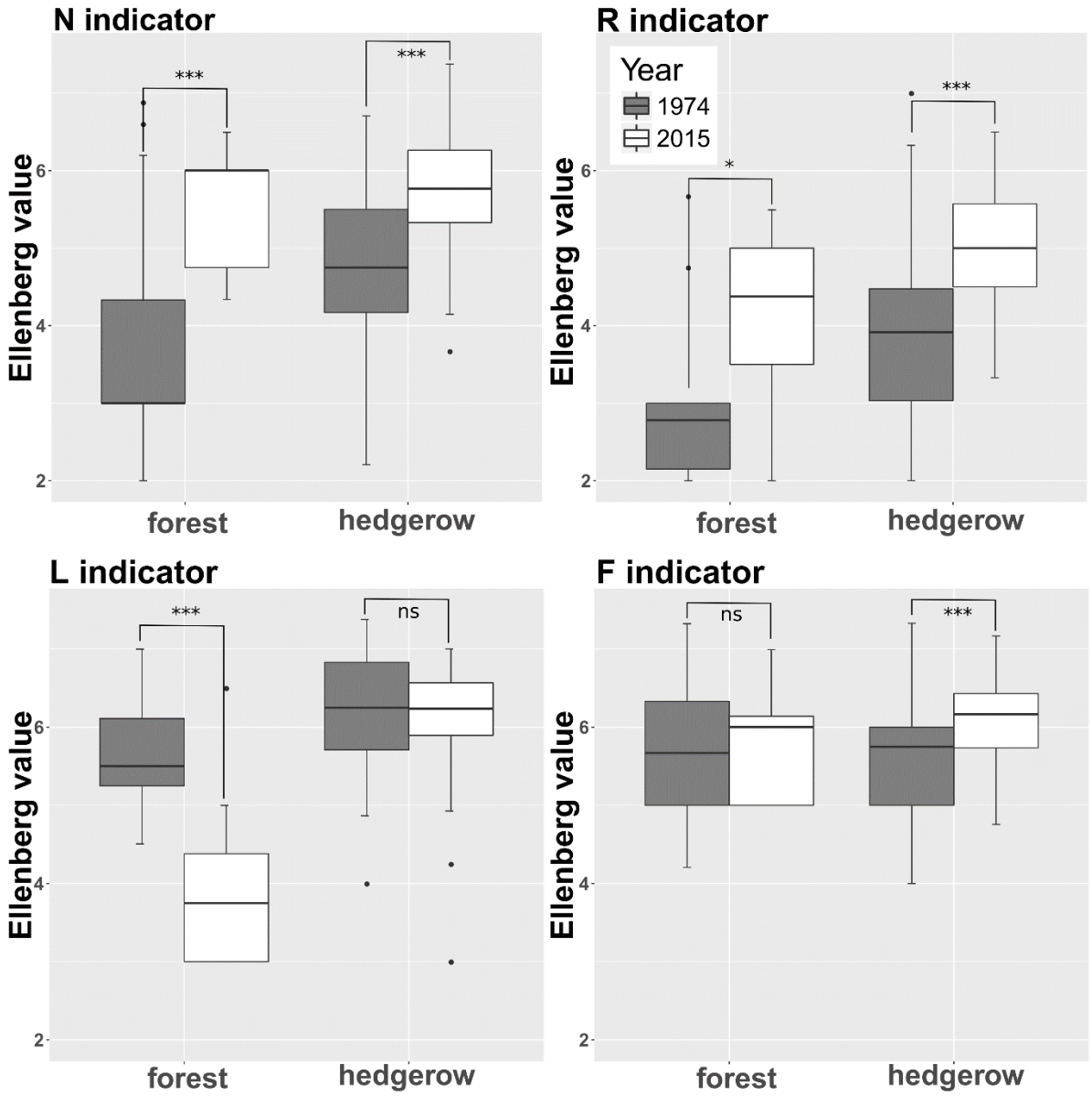

Figure 4. Shifts in Ellenberg indicator values. Changes in mean Ellenberg values for soil fertility N (a), soil reaction R (b), light L (c), and soil moisture F (d) (*sensu* Ellenberg et al. 2001) in hedgerows and forests between 1974 and 2015. The boxes indicate the 25% and 75% quartile, with a median line and 2 whiskers showing the 10% and 90% quantiles. Significant differences in mean Ellenberg values as derived from paired t-tests are indicated with asterisks (*p-value levels ns: not significant; *: p ≤ 0.05; p***: p ≤ 0.001*).

Table 1

Table 1. Diversity statistics for 1974 & 2015.

Diversity statistics for the vegetation in hedgerow plots and forest plots in 1974 and 2015: species pool (γ diversity), average species richness (α diversity ^{0}D), exponential of Shannon (α diversity 1D) and beta diversity in terms of Sørensen dissimilarity (β_{Sor}), turnover (β_{Sim}) and nestedness (β_{Nes}) are shown. For the year 1974, γ diversity is presented in absolute number of species (*cf.* original number of sampled plots *anno* 1974: hedgerows = 81; forests = 26) and in rarefied number of species (*cf.* rarefied number of sampled plots *anno* 1974: hedgerows = 54; forests = 20). The significance in differences for these statistics between the two years is indicated for the Chi squared test (Chi²), paired Wilcoxon signed-rank test (W) or paired t-test (T), where the superscripts display the p-value levels (*ns: not significant; *: $p \leq 0.05$; ***: $p \leq 0.001$*).

	1974	2015	Statistical test
	Hedgerows		
Species pool (γ diversity)	79 (*n = 81*); 70 (*n = 54*)	120 (*n = 54*)	Chi²*** (*n = 54*)
Species richness (α diversity ^{0}D)	mean = 8.69 ± 2.93 SD	mean = 13.20 ± 6.13 SD	T***
Exponential of Shannon (α diversity ^{1}D)	mean = 4.14 ± 1.54 SD	mean = 6.14 ± 3.65 SD	W***
β_{Sor}	mean = 0.72 ± 0.05 SD	mean = 0.74 ± 0.04 SD	W*
β_{Sim}	mean = 0.55 ± 0.08 SD	mean = 0.56 ± 0.07 SD	T^{ns}
β_{Nes}	mean = 0.10 ± 0.05 SD	mean = 0.12 ± 0.06 SD	W^{ns}
	Forests		
Species pool (γ diversity)	33 (*n = 26*); 30 (*n = 20*)	24 (*n = 20*)	Chi^{2ns} (*n = 20*)
Species richness (α diversity ^{0}D)	mean 5.60 ± 3.47 SD	mean 3.65 ± 2.85 SD	T^{ns}
Exponential of Shannon (α diversity ^{1}D)	mean 2.92 ± 1.97 SD	mean 2.1 ± 1.75 SD	W^{ns}
β_{Sor}	mean 0.73 ± 0.06 SD	mean 0.67 ± 0.09 SD	T*
β_{Sim}	mean 0.59 ± 0.12 SD	mean 0.52 ± 0.09 SD	T*
β_{Nes}	mean 0.14 ± 0.07 SD	mean 0.153 ± 0.04 SD	W^{ns}